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Germination and organic reserves of seeds from common Amazonian floodplain tree species

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ABSTRACT

Amazonian *várzea* floodplains (approximately 450,000 km²) are dynamic ecosystems where tree species must adapt to seasonal flooding. In this context, germination patterns and the type and composition of seed reserves (lipids, soluble sugars, proteins) are critical for seedling establishment. This exploratory study examined seed biometry, reserve composition, and germination performance in eight common tree species from high- and low-*várzea* environments: *Guazuma ulmifolia*, *Hura crepitans*, *Pseudobombax munguba*, *Nectandra amazonum*, *Zygia latifolia*, *Handroanthus barbatus*, *Macrolobium acaciifolium*, and *Crateva tapia*, aiming to contribute to the understanding of functional strategies in tropical flooded areas. Considerable interspecific variation in seed size (length: 0.31–38.03 mm; width: 0.40–36.59 mm) and reserve content was found. *Hura crepitans* and *P. munguba* had the highest lipid levels, while *H. barbatus* showed elevated concentrations of soluble sugars and proteins. The highest germination rates were observed in *H. barbatus*, *C. tapia*, and *P. munguba*, whereas *Z. latifolia* and *N. amazonum* germinated more slowly. Despite the limited number of species and sites, patterns suggest that low-*várzea* species invest more in reserves and germinate more slowly, consistent with a resource-conserving strategy for early-establishment. High-*várzea* species showed less consistent patterns, indicating the need for broader studies. Reserve composition helps explain adaptive germination responses to flooding, evidencing the complexity of these strategies. Our results provide a basis for understanding functional diversity and guide research and restoration actions in these ecosystems.

KEYWORDS: forest management, seed size, seed mass, seed reserve

Germinação e reservas orgânicas de sementes de espécies arbóreas comuns de planícies alagáveis da Amazônia

RESUMO

As várzeas amazônicas (aproximadamente 450.000 km²) são ecossistemas dinâmicos onde espécies arbóreas precisam se adaptar às inundações sazonais. Nesse contexto, os padrões de germinação e o tipo e a composição das reservas das sementes (lipídios, açúcares solúveis e proteínas) são fundamentais para o estabelecimento das plântulas. Este estudo exploratório avaliou biometria, composição das reservas e desempenho germinativo de oito espécies arbóreas comuns em ambientes de várzea alta e baixa: *Guazuma ulmifolia*, *Hura crepitans*, *Pseudobombax munguba*, *Nectandra amazonum*, *Zygia latifolia*, *Handroanthus barbatus*, *Macrolobium acaciifolium* e *Crateva tapia,* com o objetivo de contribuir para a compreensão das estratégias funcionais em áreas inundadas tropicais. Houve grande variação interespecífica no tamanho das sementes (comprimento: 0,31–38,03 mm; largura: 0,40–36,59 mm) e no conteúdo de reservas. *Hura crepitans* e *P. munguba* apresentaram os maiores teores de lipídios, enquanto *H. barbatus* teve concentrações elevadas de açúcares solúveis e proteínas. As maiores taxas de germinação foram observadas em *H. barbatus*, *C. tapia* e *P. munguba*, enquanto *Z. latifolia* e *N. amazonum* germinaram mais lentamente. Apesar do número limitado de espécies e locais, os padrões sugerem que espécies da várzea baixa investem mais em reservas e germinam mais lentamente, condizente com uma estratégia conservadora de recursos no estabelecimento inicial. Espécies da várzea alta mostraram padrões menos consistentes, indicando a necessidade de estudos mais amplos. A composição das reservas contribui para explicar as respostas germinativas adaptativas à inundação, evidenciando a complexidade das estratégias. Nossos resultados subsidiam o entendimento da diversidade funcional e orientam pesquisas e ações de restauração nesses ecossistemas.

PALAVRAS-CHAVE: manejo florestal, tamanho de sementes, massa de sementes, reserva de sementes

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INTRODUCTION

Multiple and growing stressors affect the Amazon, such as increasing human population, infrastructure development, expansion of agriculture and livestock production, as well as timber and mineral extraction, leading to unprecedented land-use changes and environmental problems in the continental-sized basin (Rodríguez and Redondo 2023). Land-use and climate change in the Amazon are growing threats to the region, which hosts a significant portion of global biodiversity, providing vital ecosystem services (Flores *et al.* 2024). Human-induced disturbances, such as dam constructions, deforestation and fires have significantly impacted the carbon balance of the Amazon (Albert *et al.* 2023).

Because rivers are still the main access routes to the Amazon region, the associated floodplain forests, especially the most fertile ones along the sediment- and nutrient-rich rivers (*várzeas*) such as the Amazon/Solimões, have historically been occupied and intensively exploited (Lopes and Piedade 2015). However, floodplain forests have specific tree communities, and it is now known that they are responsible for maintaining the region's tree diversity. Most Amazonian tree species can inhabit floodplains, but about one-sixth of Amazonian's tree diversity is ecologically specialized in floodplains (Householder *et al.* 2024).

Floodplain tree growth, phenology, and life cycles are driven by the natural flood pulse (Junk *et al.* 1989), which in the central Amazon has amplitudes of > 10 m and inundates tree roots and/or aboveground organs up to 300 days year^{-1} (Junk 1989, Wittmann *et al.* 2004). Seasonal flooding creates a dynamic environment in which plant species develop distinct strategies to ensure regeneration. Some seeds germinate rapidly after floodwater recession, taking advantage of the short terrestrial phase for establishment, whereas others exhibit flood-induced dormancy, remaining quiescent and germinating only when conditions become favorable (Scarano *et al.* 2003; Colmer and Voesenek 2009). In face of the growing detrimental human interventions in the Amazonian hydrological system affecting floodplain tree communities, there is an urgent need for an integrated approach and to increase knowledge of the regeneration mechanisms in these forests and their key fundamental functional traits.

Seed germination and early seedling establishment are critical processes for the recruitment of floodplain tree species. The success of these processes depends on a combination of environmental factors, such as flood duration and depth, oxygen availability, and soil fertility, as well as intrinsic seed traits, including size, chemical composition, and germination viability (Parolin 2001a; Wittmann *et al.* 2022). Among the most important seed traits influencing germination, seed biomass plays a fundamental role by providing essential energy reserves for germination and early seedling growth until photosynthesis can fully sustain development (Parolin 2001b). For instance, variation in seed size may reflect distinct adaptive strategies to duration of flooding closely linked to hydrological regimes and soil fertility, which impose distinct challenges for seedling survival after dispersal (Parolin *et al.* 2002).

According to the flood level gradient, Amazonian *várzea* forests are classified in low-*várzea* and high-*várzea* forests. The high-*várzea* experiences less than 3 m of flooding on average for approximately 50 days per year and is the preferred area for human activities such as housing, agriculture, and pastures, making it strongly exploited (Wittmann and Junk 2003; Schöngart and Queiroz 2010). Low-*várzea* forests experience flooding between 3-7.5 m on average accounting for up to 230 days annually (Wittmann *et al.* 2002). In low-*várzea* forests, many seeds develop mechanisms to tolerate hypoxia or enter dormancy until favorable conditions arise when the flood recedes (Colmer and Voesenek 2009; Oliveira-Wittmann *et al.* 2007). In contrast, in high-*várzea* some species adopt an escape strategy, promoting rapid hypocotyl elongation to quickly emerge above the water (Parolin *et al.* 2002). The success of germination in these environments, therefore, depends on the interaction between factors such as submersion duration, soil composition, and the availability of energy reserves within the seed, which directly influence species recruitment along the flood gradient.

Seed reserve compounds, such as lipids, soluble sugars, and proteins, play a crucial role in germination and early seedling establishment, particularly in environments subject to prolonged water stress and low soil fertility. Lipids serve as long-term energy sources, often associated with seedling survival in nutrient-poor soils and prolonged flood conditions, as observed in igapó forests (Buckeridge *et al.* 2004; Melo *et al.* 2015). Soluble sugars not only provide readily available energy but also contribute to osmotic regulation and protection against oxidative stress induced by submersion (Melo *et al.* 2015; Colmer and Voesenek 2009). Proteins, in turn, play a dual role in mobilizing stored reserves and activating metabolic processes necessary for early seedling growth following germination (Parolin 2001a). Thus, the composition and quantity of these compounds can determine germination speed and seedling establishment success, reflecting specific adaptations to the distinct environmental conditions of high- and low-*várzea* forests.

Although previous studies have addressed seed morphometry in *várzea* species, few have examined how reserve allocation contributes to adaptive germination strategies. This study adopts an exploratory approach to investigate seed size, reserve composition, and germination traits in eight tree species from high- and low-*várzea* forests near Manaus. While the sample is limited in both species number and geographic coverage, it provides important insights into functional variability in these ecosystems. Rather than testing a definitive hypothesis, we propose a working expectation: species from low-*várzea* will exhibit traits associated with resource conservation and slower germination, while high-*várzea* species will exhibit faster establishment traits associated with flood avoidance. This study thus aims to contribute to a growing understanding of functional strategies in tropical floodplain forests and provide a methodological foundation for broader future research.

MATERIAL AND METHODS

Sample Areas

The sampling of seeds was conducted in the *várzea* floodplain forests of municipalities near the city of Manaus, particularly in Careiro (3°16’S/59º59’W) and Iranduba (3°17’S/60º03’W) between March to April 2011. Mature fruits were collected from at least three individuals per species, maintaining a minimum distance of 100 meters between each tree. After collection, the fruits were preserved in plastic bags, properly labeled with the date and location of sampling and transported to the Laboratory of Ecophysiology of the MAUA (Ecology, Monitoring and Sustainable Use of Wetlands) group at INPA, Manaus.

Studied Species

Eight tree species from the *várzea* floodplain forests were selected, two from the high-*várzea* and low-*várzea* [*Guazuma ulmifolia* Lam. (Malvaceae) and *Pseudobombax munguba* (Mart. Zucc) Dugand (Malvaceae)], one from high-*várzea* [*Hura crepitans* L. (Euphorbiaceae)], and five from the low-*várzea* [*Nectandra amazonum* Ness. (Lauraceae), *Zygia latifolia* (L.) Fawcett and Rendle (Fabaceae), *Handroanthus barbatus* (E.Mey.) Mattos (Bignoniaceae), *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae), and *Crateva tapia* L. (Capparaceae)] (Wittmann *et al.* 2010). *Hura crepitans* and *G. ulmifolia* are frequent in the upper stratum of mature high-*várzea* forests, flooded between 1-3 m on average (Wittmann *et al.* 2010). *P. munguba* is a long-living pioneer tree species of the low-*várzea*, reaching ages of up to 80 years (Worbes *et al.* 1992). *Nectandra amazonum* and *C. tapia* are frequent in early successional stages of the low-*várzea* (mainly at elevations flooded between 4-6 m), while *Z. latifolia* is an understory species and *H. barbatus* is a canopy species of low-*várzea* forests, flooded between 3–5 m (Wittmann *et al.* 2010). *Macrolobium acaciifolium* is an upper canopy species of the low-*várzea*, flooded up to 7 m in height on average (Schöngart *et al.* 2005; Wittmann *et al.* 2010).

Species were classified according to wood density using data for the Amazonian floodplain, except for *Z. latifolia* and *G. ulmifolia*, where data from tropical South America were used (Zanne *et al.* 2009). Wood density was classified accord to Schöngart (2008) as low-density for values below 0.6 g cm^{-3}, and heavy or high-density wood for values above 0.6 g cm^{-3} (Table 1).

Based on seed moisture content at dispersal and ecological characteristics reported in the literature (e.g. Conserva *et al.* 2013), four species examined in this study, specifically *Crateva tapia*, *Macrolobium acaciifolium, Handroanthus barbatus* and *Nectandra amazonum* can be classified as bearing recalcitrant seeds (Table S1). These species typically display high sensitivity to desiccation and rapid post-dispersal germination, consistent with adaptive strategies in flood-prone environments.

Morphological Description of Seeds

From the homogenized seed group, belonging to three mother plants per species, 50 fresh seeds were randomly selected (n = 50) per species. Seeds were weighed and measured in length using a digital caliper (Kingtools model) with an accuracy of 0.01 mm and a semi-analytical balance (Bel Mark 1000) with a maximum and minimum capacity of 1000 g and 200 mg, respectively.

Seeds Reserve Content

Quantitative characterization of organic reserves was conducted on the seed kernel, comprising the embryo and cotyledons, of quiescent seeds. For each species, 100 seeds were used in the biochemical analyses, divided into four biological replicates of 25 seeds each. For lipid extraction, the total dry mass per replicate ranged between 0.8–1.2 g, depending on seed size. Protein and carbohydrate analyses were performed using subsamples of the same replicates. This approach ensured analytical robustness while accounting for

Table 1. Wood density and classification of Amazonian floodplain tree species. WD: wood density (g cm^{3}), DC: Density Classification, E: environment, P: Phenotype, SD: Seed dispersal, RWI: Radial wood increment (mm^{-1} year).

Species	WD	DC	E	P	SD	RWI	Reference
Crateva tapia	0.49 ± 0.05	low	LV	Perennial	Water and fish	9.6 ± 1.0	Parolin and Ferreira 1998
Guazuma ulmifolia	0.51 ± 0.04	low	HV/LV	Semi-deciduous	Birds	19 ± 0	Almeida-Cortez 2004
Handroanthus barbatus	0.83 ±0.08	high	LV	Deciduous	Wind and water	3.4 ± 1.0	Fonseca-Júnior *et al.* 2009
Hura crepitans	0.38 ± 0.09	low	HV	Perennial	Wind and water	18.1 ± 0.4	Wittmann *et al.* 2006
Macrolobium acaciifolium	0.45 ± 0.03	low	LV	Deciduous	Water and fish	10.4 ± 2.6	Schöngart *et al.* 2005
Nectandra amazonum	0.44 ± 0.07	low	LV	Deciduous	Water and fish	14.7 ± 2.2	Wittmann *et al.* 2006
Pseudobombax munguba	0.23 ± 0.04	low	HV/LV	Deciduous	Wind, water, and fish	13.5 ± 2.5	Schöngart 2003; Wittmann *et al.* 2004
Zygia latifolia	0.75 ± 0.02	high	LV	Perennial	Water	-	Monteiro *et al.* 2022

LV = low-*várzea*; HV = high-*várzea*.

inter-individual variation. Samples were dried at 45°C until reaching a constant weight, and then ground in a crucible for subsequent lipid, total soluble sugars (TSS), and protein analyses. Lipid extraction was performed using the Soxhlet extraction method with four replicates, following the protocol described by Ramadan *et al.* (2009). Carbohydrates were extracted using the methanol-chloroform-water method in a ratio of 12:5:3 (v/v/v). For soluble sugar (TSS) quantification, 5 ml of anthrone reagent was added to the supernatant, and the absorbance was measured at 625 nm using a spectrophotometer (Krotron Uvikon 930) according to the method of Dubois *et al.* (1956). Protein content was quantified using the Bradford assay (Bradford 1976), where Coomassie Brilliant Blue dye was added to the protein extract, and absorbance was recorded at 595 nm with a spectrophotometer.

Seed Germination and Seedling Emergence

After fruit collection, seeds were processed within 24 hours. Germination experiments were conducted in the greenhouse of the INPA/MAUA between April and November 2011, for 120 days per species (Figure SI1). The nursery had 11% solar radiation, with average temperatures ranging from 24.4°C to 34.5°C during the experimental period. Seeds were sown in trays measuring 35 cm (length) x 20 cm (width) x 7 cm (depth), using alluvial soils sampled in the studied floodplain. Four replicates of 25 seeds per species were used.

Germination was considered when radicle protrusion was observed, which corresponds to the end of phase II of water uptake (Bewley and Black 1994). The germination parameters evaluated were: germination percentage (%G), mean germination time (MGT), and germination speed index (GSI). Germination percentage (%G) represents the proportion of seeds that germinated during the experiment and was calculated as $\%G = 100\ x\ \frac{number\ of\ germinated\ seeds}{total\ number\ of\ seeds}$ (Bewley and Black 1994). The mean germination time (MGT) which is the average time required for seeds to germinate (days) was calculated as $MGT = \frac{\Sigma(ni * ti)}{\Sigma ni}$ where ni is the number of seeds germinated at time ti, calculated in days since the beginning of the experiment (Ranal and Santana 2006). The germination speed index (GSI) reflecting the speed of germination, was calculated as $GSI = \Sigma \frac{ni}{ti}$ (Maguire 1962).

Seedling emergence was also evaluated based on emergence percentage (%E), mean emergence time (MET), and emergence speed index (ESI). Emergence percentage was defined as the proportion of seeds that produced emerged seedlings and was calculated as $\%E = 100\ x\ \frac{number\ of\ emergence\ seedlings}{total\ number\ of\ seeds}$ (Bewley and Black 1994). Mean emergence time (MET), the average time required for seedlings to emerge, was calculated as $MET = \frac{\Sigma(ni * ti)}{\Sigma ni}$, where: ni represents the number of emerged seedlings at time ti, calculated in days since the beginning of the experiment (Ranal and Santana 2006). The seedling emergence speed indices (ESI) that reflecting the speed of seedling emergence, was calculated as $ESI = \Sigma \frac{ni}{ti}$ (Maguire 1962).

All germination and emergence parameters were monitored daily throughout the 120-day experimental period.

Data analysis

To assess how the metrics described above differ between species, normality was checked with the Shapiro-Wilk test. As the data did not show normal distribution, they were transformed by square root. For data that still did not show a normal distribution after transformation, the non-parametric Mann-Whitney test was used to compare the means. For data that showed a normal distribution, Student's t-test was applied to compare the means. In addition, the correlation between the seed metrics, germination index, and wood density was evaluated using the Pearson's correlation test. This test was chosen to measure the strength and direction of linear relationships between variables. The significance level was set at $p < 0.05$ for all analyses. Fresh biomass, TSS, proteins, GSI and MGT had their data log-transformed to normalize the dataset. All statistical analyses were performed using R (version 4.0.2, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Seed Morphometry and Organic Reserves

The lowest values for fresh biomass and seed morphometric characteristics were observed in the high-*várzea* species *G. ulmifolia* and the low-*várzea* species *P. munguba* and *C. tapia*. The low-*várzea* species *N. amazonum, M. acaciifolium* and *Z. latifolia*, exhibited the highest fresh biomass values (Tables 1 and 2, Figure SI 2).

Among the studied species, the highest lipid concentrations relative to dry weight were recorded for *H. crepitans* (554.55 mg g^{-1}) and *P. munguba* (423.23 mg g^{-1}), which were significantly greater than those of the other species (Table 3). In contrast, *M. acaciifolium* and *Z. latifolia* had the lowest lipid concentrations (8.43 mg g^{-1}; 3.64 mg g^{-1}, respectively), with no statistical differences between them (Table 3). The highest concentration of total soluble sugars (TSS) was found in *H. barbatus* (53.85 mg g^{-1}). Intermediate concentrations were observed in *Z. latifolia* (35.36 mg g^{-1}) and *H. crepitans* (33.98 mg g^{-1}). The remaining species exhibited lower TSS levels, ranging from 18.21 to 23.52 mg g^{-1}, with no significant differences among them (Table 3). Protein's relative to dry weight were significantly higher in *H. crepitans* (427.49 mg g^{-1}) and *H. barbatus* (331.66 mg g^{-1}). Intermediate values were observed for *P. munguba,* and *C. tapia,* while the lowest concentrations were recorded for *Z. latifolia* and *G. ulmifolia* (Table 3).

Table 2. Average values (± standard deviation) of seed length, width, thickness, and fresh mass (n = 100) of eight commom Amazonian floodplain tree species.

Family	Species	Length (mm)	Width (mm)	Thickness (mm)	Fresh Mass (mg)
Capparaceae	*Crateva tapia*	9.74±0.68	9.09±0.56	4.97±0.47	31.70±1.31
Malvaceae	*Guazuma ulmifolia*	0.31±0.46	1.90±0.17	1.80±0.14	6.40±1.07
Euphorbiaceae	*Hura crepitans*	21.44±1.61	20.11±1.51	5.85±0.56	88.41±2.68
Bignoniaceae	*Handroanthus barbatus*	38.03±9.26	14.78±1.61	3.81±0.51	623.80±122.69
Fabaceae	*Macrolobium acaciifolium*	26.89±1.74	15.48±1.12	15.48±1.12	4042.70±591.40
Lauraceae	*Nectandra amazonum*	33.33±2.49	36.59±2.66	5.84±0.98	4304.10±1008.20
Malvaceae	*Pseuddobombax munguba*	0.50±0.08	0.40±0.07	0.30±0.09	24.32±1.71
Fabaceae	*Zygia latifolia*	25.50±2.14	27.19±2.14	6.54±1.09	2412.00±427.50

Table 3. Average values of lipids, total soluble sugars (TSS), and proteins in seeds of eight Amazonian floodplain tree species. Means within the same column followed by the same letter are not significantly different according to Tukey's test at the 5% probability level.

Species	Lipids (mg g^{-1})	Lipids%	TSS (mg g^{-1})	TSS%	Proteins (mg g^{-1})	Proteins %
Crataeva tapia	330.48^{b}	77.11%	18.21 ^{c}	2.5%	146.39^{b}	20.4%
Guazuma ulmifolia	96.19^{d}	69.6%	18.22 ^{c}	13.2%	23.76^{d}	17.2%
Hura crepitans	554.55^{a}	54.6%	33.98 ^{b}	3.3%	427.49^{a}	42.1%
Handroanthus barbatus	192.23^{c}	77.9%	53.85 ^{a}	4.3%	331.66^{a}	17.7%
Macrolobium acaciifolium	8.43^{e}	33.3%	22.66 ^{c}	9.3%	71.25^{bc}	57.4%
Nectandra amazonum	123.53^{c}	8.2%	20.63 ^{c}	22.1%	84.78^{bc}	69.6%
Pseudobombax munguba	423.23^{a}	54.0%	23.52 ^{c}	9.0%	96.38^{b}	37.0%
Zygia latifolia	3.64^{e}	4.0%	35.36 ^{b}	38.6%	52.59^{cd}	57.4%

Germination and Emergence

Germination percentages differed between species (t = 3.656; df = 6; p = 0.011; n = 4), with the highest germination percentages observed for *H. barbatus* (99%), *C. tapia* (95%) and *P. munguba* (91%). The mean germination time varied significantly among species (t = -10.954; df = 6; p = 0.000; n = 4), with *Z. latifolia* and *N. amazonum* exhibiting the longest germination time (mean MGT of 64.01 and 27.32 days, respectively). The germination speed index values (GSI) also varied among species (t = 15.274; df = 6; p = 0.000; n = 4). *P. munguba* had the highest GSI value, germinating approximately six times faster than most other species. The emergence percentage was significantly lower for *Z. latifolia* (13%) compared to the other species (U = 4.500; p = 0.282; n = 4).

Mean emergence time also varied among species (t = -14.652; df = 6; p = 0.000; n = 4). Longer emergence times were observed for *Z. latifolia* (mean MET 68.1 days), *N. amazonum* (44.67 d), *H. crepitans* (34.71 d) and *M. acaciifolium* (37.26 d). Additionally, the emergence speed index (ESI) showed significant differences between species (t = 22.600; df = 6; p = 0.0001; n = 4) with *Z. latifolia* (0.079) displaying considerably lower values than the other species (Table 4).

Table 4. Means values of germination rate (G%), germination speed index (GSI), mean germination time (MGT), emergence (E%), emergence speed index (ESI), and mean emergence time (MET) for Amazonian floodplain tree species. Means within the same column followed by the same letter are not significantly different according to Tukey's test at the 5% probability level.

Species	G (%)	GSI	MGT	E (%)	ESI	MET
Crateva tapia	95^{a}	2.320^{a}	11.78^{b}	94^{a}	1.330^{a}	18.37^{b}
Guazuma ulmifolia	61^{a}	1.260^{a}	17.13^{b}	38^{a}	0.646^{a}	17.99^{b}
Handroanthus barbatus	99^{a}	1.882^{a}	16.49^{b}	94^{a}	1.225^{a}	20.71^{b}
Hura crepitans	88^{a}	1.000^{a}	24.05^{b}	97^{a}	0.650^{a}	34.71^{a}
Macrolobium acaciifolium	53^{a}	0.629^{a}	23.89^{b}	45^{a}	0.326^{a}	37.26^{a}
Nectandra amazonum	25^{a}	0.289^{a}	27.32^{a}	20^{a}	0.125^{a}	44.67^{a}
Pseudobombax munguba	91^{a}	6.195^{a}	4.54^{c}	86^{a}	3.005^{a}	07.60^{b}
Zygia latifolia	17^{b}	0.166^{b}	64.01^{a}	13^{b}	0.079^{b}	68.09^{a}

Correlation Analysis

The correlation analysis revealed significant relationships between seed traits and germination metrics (Table 5). Seed width was positively correlated with seed length (r = 0.78, p = 0.02) and protein percentage (r = 0.76, p=0.03), but negatively with lipid percentage (r = -0.76, p=0.03). Fresh biomass showed significant positive correlations with seed width (r = 0.72, p = 0.04) and thickness (r = 0.72, p = 0.04). Lipid percentage was negatively correlated with both TSS (r = -0.83, p = 0.01) and protein percentage (r = -0.94, p < 0.001). No significant correlations with wood density were observed.

Germination percentage was negatively correlated with fresh biomass (r = 0.77, p = 0.027), TSS% (r = -0.90, p < 0.001) and proteins% (r = -0.76, p = 0.03). Mean germination time was positively correlated with TSS% (r = 0.86, p = 0.01) but negatively correlated with G% (r = -0,78, p = 0.02) and lipids percentage (r = -0.75, p < 0.001).

Emergence percentage (%E) was negatively correlated with TSS% (r = -0.86, p = 0.006), and positively with G% (r = 0.97, p < 0.001). ESI was strongly correlated positively with GSI (r =0.97, p < 0.001). Lastly, MET showed positive correlations with MGT (r = 0.95, p < 0.001) and negative correlations with lipids percentage (r = -0.84, p = 0.008), % G (r = -0.83, p = 0.01), GSI (r = -0.73, p = 0.03), and ESI (r = -0.77, p = 0.02). No significant correlations were found for the other parameters (Table 5).

DISCUSSION

The results of this study highlight significant interspecific differences in seed reserve composition and germination traits among Amazonian floodplain tree species. These findings partially align with our initial hypothesis that species occupying different floodplain environments exhibit distinct seed reserve composition and germination strategies, reflecting adaptive responses to flooding regimes.

Our hypothesis predicted that species from high-*várzea* would exhibit reserve compositions favoring rapid germination and establishment, whereas those from environments facing prolonged submersion (low-*várzea*) would invest in reserves that enhance tolerance to flooding stress. For instance, *H. crepitans,* a high-*várzea* species, demonstrated the high lipid percentage (54.6%), a trait commonly associated with prolonged seed viability and resilience in high dynamic environments (Melo *et al.* 2015; Ferreira *et al.* 2017; Conserva *et al.* 2018). This high lipid content is crucial for desiccation tolerance, as evidenced by its ability to germinate after desiccation periods (Conserva *et al.* 2013). Similar lipid-rich traits were observed in *P. munguba* (54.0%) and *C. tapia* (77.1%), suggesting that lipids may also be advantageous adaptations to low-*várzea* conditions characterized by prolonged submersion (Conserva *et al.* 2018).

Interestingly, mean germination time and mean emergence time were negatively correlated with lipids percentage, suggesting that lipid reserves play a crucial role in both germination and post-germination establishment

Table 5. Pearson Correlation between seed parameters, germination index, and wood density (r/p-value). Wood density (WD). Germination rate (G%), germination speed index (GSI), mean germination time (MGT), emergence (E%), emergence speed index (ESI), and mean emergence time (MET).

	WD	Length	Width	Thickness	Fresh Mass	Lipids%	TSS%	Proteins%	G (%)	GSI	MGT	E (%)	ESI	MET
WD		0.14	0.49	0.85	0.84	0.98	0.42	0.66	0.67	0.21	0.19	0.64	0.28	0.32
Length (mm)	0.57		0.02	0.21	0.11	0.33	0.63	0.27	0.48	0.12	0.29	0.67	0.15	0.15
Width (mm)	0.29	0.78		0.33	0.04	0.03	0.16	0.03	0.07	0.06	0.08	0.20	0.05	0.01
Thickness (mm)	0.08	0.50	0.39		0.05	0.32	0.86	0.17	0.38	0.14	0.43	0.49	0.13	0.22
Fresh Mass (mg)	0.08	0.61	0.72	0.71		0.02	0.20	0.01	0.03	0.16	0.25	0.05	0.11	0.08
Lipids(%)	-0.01	-0.39	-0.76	-0.41	-0.80		0.01	<0.001	<0.001	0.28	0.03	0.02	0.18	0.01
TSS(%)	0.33	0.20	0.55	0.08	0.51	-0.83		0.12	<0.001	0.32	0.01	0.01	0.23	0.02
Proteins(%)	-0.19	0.45	0.76	0.54	0.85	-0.94	0.60		0.03	0.34	0.15	0.10	0.24	0.04
G(%)	-0.18	-0.30	-0.67	-0.36	-0.77	0.90	-0.90	-0.76		0.11	0.02	<0.001	0.06	0.01
GSI	-0.50	-0.60	-0.69	-0.57	-0.55	0.44	-0.40	-0.39	0.61		0.08	0.15	<0.001	0.04
MGT	0.52	0.42	0.66	0.33	0.46	-0.75	0.86	0.55	-0.78	-0.65		0.06	0.06	<0.001
E(%)	-0.20	-0.18	-0.51	-0.29	-0.71	0.80	-0.86	-0.63	0.97	0.56	-0.68		0.08	0.05
ESI	-0.44	-0.55	-0.71	-0.58	-0.61	0.52	-0.48	-0.47	0.70	0.99	-0.68	0.65		0.02
MET	0.40	0.56	0.82	0.49	0.65	-0.84	0.81	0.73	-0.83	-0.74	0.96	-0.70	-0.78	

in floodplain ecosystems (Mori *et al.* 2019; Carvalho *et al.* 2024). This highlights the complex interplay between seed traits and environmental adaptations in floodplain ecosystems. For instance, buoyant seeds germinate rapidly upon contact with water, while submerged seeds may experience dormancy until floodwaters recede, highlighting the adaptive significance of lipid reserves for energy during these critical phases (Wittmann *et al.* 2009; Melo *et al.* 2015).

In the present study lipids were the primary reserve component followed by proteins and soluble carbohydrates. Seeds analysis indicate that lipids serve as the primary reserve component in many species, crucial for germination and early seedling development, as they provide a dense energy source (McDonald *et al.* 2024). The mobilization of these reserves varies among species, exemplified by *C. tapia* efficient reserve utilization for rapid seedling growth, contrasting with *H. crepitans*, which invests in larger reserves for better establishment under less favorable conditions (Richardson 2020; Carvalho *et al.* 2024). This diversity in seed reserve allocation strategies reinforces the hypothesis that the success of tree species in *várzea* environments is tightly linked to their ability to optimize the timing and efficiency of germination and seedling establishment in response to variable flood pulses.

The high protein percentage in *M. acaciifolium* (57.4%) slow-growing species inhabiting the late-successional stratum of highly flooded *várzea* forests, may be linked to their tolerance to environmental stress, as proteins play critical roles in stress response mechanisms, including osmotic adjustment and antioxidant defense (Tellah 2022). However, no clear relationship was observed between protein percentage and germination speed or mean germination time (MGT), suggesting that other factors, such as seed morphology or environmental conditions, may interact with reserve composition to influence germination dynamics (Oguz *et al.* 2022).

The abundance of proteins in *M. acaciifolium* seeds, which require a prolonged mean emergence time (MET) of 37.26 days, suggests a strategy for enduring less favorable conditions, as proteins are crucial for embryo development and support seedling growth until autotrophy is achieved (Bera *et al.* 2023). In contrast, *P. munguba* exhibits a lower protein percentage but achieves a high germination performance of 91% and lower MET (7.6 days), indicating that its reserve mobilization is optimized for rapid seedling development rather than long-term survival (Bera *et al.* 2023). Overall, the balance between protein reserves and germination efficiency reflects adaptive strategies in seed survival and growth under varying environmental conditions. Additionally, the response of seed proteins to abiotic stresses, such as drought, highlights their importance in seed viability and resilience (Sharma *et al.* 2022).

The relationship between total soluble sugars (TSS) and germination traits appears complex, as evidenced by findings that species with higher TSS, such as *Z. latifolia* and *M. acaciifolium*, exhibited slower germination rates compared to those with lower TSS, like *H. crepitans* and *P. munguba*. This suggests that while carbohydrates are crucial for seed germination and early growth, their role may be influenced by other factors, including seed morphology and environmental conditions (Sami *et al.* 2016). Correlation analyses indicate a negative relationship between germination percentage and fresh biomass, alongside a positive correlation with TSS, highlighting the multifactorial nature of germination dynamics. Additionally, the mobilization of seed reserves, including carbohydrates, is essential for seedling vigor, emphasizing the need for a holistic understanding of seed reserve dynamics during germination (Sami *et al.* 2016).

The germination performance varied widely among species, reflecting distinct ecological strategies. For example, *P. munguba* exhibited the fastest germination (MGT: 4.54 days), potentially linked to an escape strategy in high-*várzea* (Parolin *et al.* 2002). In contrast, species such as *N. amazonum* and *Z. latifolia* showed slower germination rates (MGT: 27.32 and 64.01 days, respectively), which may reflect strategies to synchronize germination with optimal environmental conditions, consistent with the tolerance strategy also described by Parolin *et al.* (2002).

Seed morphological traits also played a role in germination dynamics. For instance, species with larger seed dimensions, such as *M. acaciifolium* and *N. amazonum*, generally exhibited slower germination (GSI), likely due to higher resource allocation to seedling development (Polli *et al.* 2020). On the other hand, small seeds such as *C. tapia* and *P. munguba* exhibited rapid germination. Correlation analysis revealed that fresh biomass was negatively associated with GSI but positively correlated with mean germination time underscoring the trade-offs between seed size and germination speed (Geritz *et al.* 2018).

Although no significant overall correlations were found between wood density and germination or emergence parameters, species-specific trends (e.g. fast-germinating species with low wood density) suggest that wood density might still be related to early developmental traits in certain ecological contexts (Yang *et al.* 2024). This reinforces the complexity of ecological interactions and underscores the need for further studies integrating phylogenetic relationships, field conditions, and environmental factors such as inundation regimes and soil fertility.

Crateva tapia exhibit rapid germination and emergence, traits advantageous for low-*várzea* environments characterized by prolonged submersion, allowing it to capitalize on transient conditions and reduce mortality risk (Oliveira-Wittmann *et al.* 2007; Polli *et al.* 2020). The higher germination percentage and faster emergence values (ESI) of *C. tapia* indicate that its seeds are well adapted to benefit from brief favorable conditions, potentially reducing the risk of mortality during extensive floods (Junk *et al.* 1989; Norden *et al.* 2008). This suggests that seed size and reserve content alone do not fully explain germination success, as the timing and efficiency of seedling establishment play crucial roles (Ferreira *et al.* 2009). Conversely, *N. amazonum* displays wide variation in germination and emergence success, likely tied to its ichthiocory strategy for seed dispersal (Alencar-Maia and Jackson 2000). This strategy, where fish play a crucial role in transporting seeds, enhances the establishment of seedlings in the dynamic and often unstable conditions of Amazonian *várzea* floodplains. Research indicates that the effectiveness of fish as seed dispersers varies by species, with larger frugivorous fish generally being more effective due to their ability to transport larger seeds without damaging them (Costa *et al.* 2023; Weiss *et al.* 2023). Additionally, the timing of seed release coincides with flooding events, allowing seeds to float and germinate once water levels recede, thus capitalizing on the hypoxic conditions that may break dormancy (Kubitzki and Ziburski 1994). This adaptation to environmental variability underscores the evolutionary significance of ichthyochory in promoting plant recruitment in these ecosystems (Van Den Elzen *et al.* 2023).

Our results partially support the proposed hypothesis by demonstrating that germination strategies reflect distinct environmental adaptations, contributing to the coexistence of species in different *várzea* niches. This pattern highlights the importance of energy reserves in species' responses to fluctuations in the hydrological regime. The ecological implications of these findings extend to recruitment dynamics in Amazonian floodplain forests. Species with fast germination and establishment rates, such as *P. munguba*, may dominate early successional stages, particularly in disturbed or open areas (Witmann *et al.* 2010). Conversely, slower-germinating species with higher wood density, such as *Z. latifolia*, may contribute to long-term forest structure and resilience. The positive correlation between wood density and MGT further supports the role of seed traits in shaping ecological strategies and forest composition over time. Therefore, understanding the physiological and morphological mechanisms that drive seed establishment success is fundamental to managing floodplain regeneration.

The variability in seed germination traits and reserve composition among floodplain tree species highlights the importance of species-specific approaches in restoration and conservation initiatives. For instance, fast-germinating species with low wood density, such as *P. munguba*, may be prioritized for rapid canopy closure in degraded areas. Conversely, slower-germinating species with high wood density, such as *Z. latifolia*, may play a pivotal role in enhancing structural diversity and long-term carbon storage.

Despite the potential applications of these findings, this study primarily addresses germination dynamics under natural conditions and does not explicitly assess their implications for restoration practices. Future studies should explore how these traits translate to field performance under varying environmental and microhabitat conditions, including inundation regimes and soil fertility gradients. Additionally, integrating seed reserve data with seedling survival and growth metrics would provide a more comprehensive understanding of species' adaptive strategies and their potential roles in ecosystem recovery.

CONCLUSIONS

This study revealed notable interspecific variability in seed reserve composition and germination traits among common tree species from Amazonian *várzea* floodplains, providing initial evidence that reserve allocation plays a functional role in early establishment under variable flood regimes. While the hypothesized associations between flooding gradients and germination strategies were only partially supported, the findings contribute to our understanding of how species-specific seed traits mediate adaptation to dynamic floodplain environments. These insights advance the understanding of life-history strategies in flood-prone ecosystems and offer a practical foundation for selecting suitable species for restoration in degraded *várzea* areas, particularly in the face of ongoing climate-induced hydrological changes.

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SUPPLEMENTARY MATERIAL

Lopes *et al.* Germination and organic reserves of seeds from common Amazonian floodplain tree species

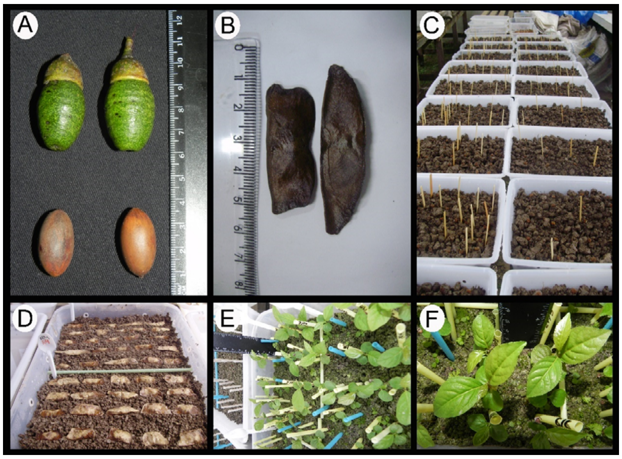

Figure S1. Steps to obtain germination data from common Amazonian floodplain tree species. **A** – Step 1: fruit collection (fruits and seeds of *Nectandra amazonum*); **B** – Step 2: seeds' biometrics measurements (*Handroanthus barbatus* seeds that have been measured and screened for germination); **C** to **F** – Step 3: Germination experiments (trays used for the experiments where each seed/seedling was marked with small sticks; *H. barbatus* germination trays (C-D), and *Guazuma ulmifolia* seedlings at different germination times (E-F)). Credits for images: Elizabeth Rebouças.

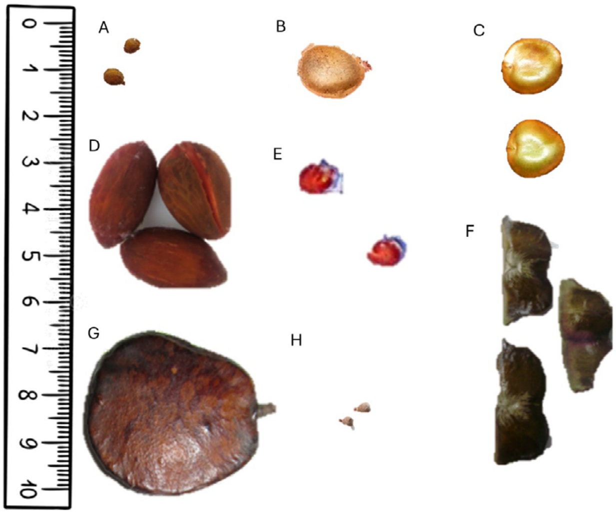

Figura S2. Seed size variation of eight common Amazonian floodplain tree species: **A**) *Pseudobombax munguba*; **B**) *Hura crepitans*; **C**) *Zygia latifolia*; **D**) *Nectandra amazonum*; **E**) *Crateva tapia*; **F**) *Handroanthus barbatus*; **G**) *Macrolobium acaciifolium*; **H**) *Guazuma ulmifolia*. Photos: Elizabeth Rebouças.

Table S1. Classification of seeds according to storage behavior (orthodox vs. recalcitrant).

Species	Classification	Reference
Crateva tapia	Recalcitrant	Alves *et al.* 2017
Guazuma ulmifolia	Orthodox	Carvalho *et al.* 2006
Handroanthus barbatus	Recalcitrant	Conserva *et al.* 2013
Hura crepitans	Orthodox	Conserva *et al.* 2013
Macrolobium acaciifolium	Recalcitrant	Maia *et al.* 2005
Nectandra amazonum	Recalcitrant*	Carvalho *et al.* 2008
Pseudobombax munguba	Orthodox	Marques 2019
Zygia latifolia	Recalcitrant*	Ståhl *et al.* 2004

* Information refers to another species of the same genus *(Nectandra grandiflora, Nectandra lanceolata, Nectandra oppositifolia; Zygia nubigena).*

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